Chrysolepidae were encountered as follows: *Q. palmeri* Engelm. at 2800 to 4000 feet. *Q. chrysolepis* Liebm. at 5500 to 7500 feet, and an anomalous entity suggesting *Q. chrysolepis* at 7000 to 9650 feet. With the possible exception of *Q. chrysolepis,* these San Pedro Mártir species would not be expected to have contributed the aberrations of the San Vicente populations, and the presence in the San Pedro Mártir of typical *Q. cedrosensis* makes even this extremely unlikely.

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PARASITISM IN PEDICULARIS [1]

Elizabeth F. Sprague

The parasite-host relationship for many European species of *Pedicularis* has been well-documented by Wettstein (1891), Boeshore (1920), Hayek and Hegi (1918), and others. Such parasitism accounts for the difficulty in culture noted by such workers as Don (1838) and Tsoong (1955), although a few species have been cultivated and a few are sold for ornamental value. Tsoong (*loc. cit.*) states that *P. fletcheriana* Tsoong "may be easily raised from seed" and that at Perthshire, England, it established itself and freely reproduced. This indicates that at least some species under gven conditions may be saprophytic, mycorrhizal, or completely autotrophic. Sperlich (1902) found some species of *Pedicularis* to be both parasitic and saprophytic, with haustoria of the same plant attached to both dead organic matter and living roots. Certainly many of the meadow-dwelling species are quite opportunistic with regard to available host plants. In Europe, *P. sylvatica* L., and, in America, *P. canadensis* L. and *P. lanceolata* Michx. are regularly sold and cultivated without apparent hosts. They probably thrive as saprophytes

[1] This paper is adapted from a portion of a doctoral dissertation prepared at the Rancho Santa Ana Botanic Garden and the Claremont University College, Claremont, California. I wish to acknowledge the assistance of Doctors Verne Grant, Sherwin Carlquist, and Philip A. Munz. The illustrations were prepared with the assistance of Messrs. William Klein and C. Dodson. The research was partially financed by two grants from the Claremont University College, Claremont, California, and a fellowship from the Southern Fellowships Fund, Chapel Hill, North Carolina. A grant from the University Center, Richmond, Virginia, assisted with typing and photographic expenses.

because a soil rich in humus is required, although even then they may be difficult to maintain. Attempts to grow thirteen plants of *P. canadensis* at Rancho Santa Ana Botanic Garden, Claremont, California, were not successful either in the greenhouse or in deep humus under *Quercus agrifolia* Neé. Only four to six small leaves per plant were produced, and only five plants persisted to the second year.

Attention was focused on the parasitic nature of seven California species when an attempt was made to cultivate them for experimental purposes. Plants of *Pedicularis densiflora, P. semibarbata, P. groenlandica, P. attollens,* and *P. dudleyi* were transplanted to clay pots and grown in the glasshouse at Rancho Santa Ana Botanic Garden, Claremont, California. None bloomed and even those which were accompanied by associated plants produced only a very few small leaves the second season. A single plant of *P. dudleyi* was grown successfully for the two-year period. Its native habitat, the redwood forest, was probably more successfully simulated under greenhouse conditions.

No species of *Pedicularis* is recorded as requiring exact host specificity even as to genus, but some do "show obvious preference for definite species" (Hayek and Hegi, 1918, page 112, the quotation a translation from the German). The majority of European species are meadow-dwelling and hence the hosts listed are various grasses, sedges and willows; however, Hayek and Hegi note that *P. recutita* L. is found usually on *Deschampsia caespitosa* (L.) Beauv. and *Pedicularis verticillata* L. on *Sesleria caerulaea* Scop. For the California species examined in this study, field observation and laboratory verification indicated the host relationships shown in Table 1. The alpine and meadow species of the Sierra Nevada, *Pedicularis attollens, P. groenlandica* and *P. crenulata,* show typical facultative association with various meadow plants. A fourth Sierran species, *P. racemosa*, grows in deep humus associated with *Abies concolor* and *Pinus monticola*; no haustorial connections were identified. *Pedicularis dudleyi* is associated with such redwood-forest understory plants as *Vaccinium ovatum* and *Lithocarpus densiflora*; roots were not observed.

However facultative the parasite-host relationship may appear to be in most species, observations on *Pedicularis densiflora* and *P. semibarbata* show restrictions unlike those reported for other species. These two species parasitize principally roots of trees or woody shrubs. In addition, there is evidence that the local populations of *P. densiflora* are physiologically distinct. In southern California, *P. densiflora* is associated primarily with *Adenostoma fasciculatum;* in the Santa Lucia Mountains, some populations are associated with *Pinus coulteri* and *Arbutus menziesii,* others with *Adenostoma* and *Arctostaphylos;* in the San Francisco area, *Arbutus menziesii* and *Quercus kelloggii* are the conspicuous hosts except on the top of Mount Diablo, where *Pedicularis* grows in a pure stand of *Adenostoma*. In the two areas on Mount Diablo and in the

Table 1. Hosts at Various Localities of Observation for Five Species of Pedicularis[1]

(Probable host—P. Confirmed host—C.)

Pedicularis Species	Locality	Host
P. densiflora subsp. *densiflora* Benth.	Del Mar mesa, San Diego County	(C) *Adenostoma fasciculatum* H. & A. (P) *Arctostaphylos glandulosa* var. *crassifolia* Jepson
	Cobal Canyon, San Gabriel Mountains, Los Angeles County	(C) *Adenostoma fasciculatum*
	Topanga Canyon, Santa Monica Mountains, Los Angeles County	(C) *Adenostoma fasciculatum*
	Refugio Canyon burn, San Marcos Pass, Santa Barbara County	(C) *Adenostoma fasciculatum* (P) *Arctostaphylos glandulosa* Eastw.
	Klau Mine on serpentine, Adelaide, San Luis Obispo County	(P) *Adenostoma fasciculatum*
	Marquart Ranch, Cambria-Adelaide Road, Santa Lucia Range, San Luis Obispo County	(P) *Arbutus menziesii* Pursh. (?) *Pinus coulteri* Don.
	7X Ranch pass, on serpentine, Santa Rita Canyon, Santa Lucia Range, San Luis Obispo County	(C) *Adenostoma fasciculatum* (?) *Quercus dumosa* Nutt. (?) *Arctostaphylos* sp. (?) *Rhus diversiloba* T. & G. (?) *Diplacus puniceus* Nutt.
	La Honda, Santa Cruz Mountains, San Mateo County	(P) *Arbutus menziesii* (P) *Rhus diversiloba* (P) *Diplacus aurantiacus* Jepson
	Phoenix Lake, Marin County	(P) *Arbutus menziesii* (P) *Quercus kelloggii* Newb.
	Mount Diablo, Toyon Road, Rocky Point, Contra Costa County	(C) *Adenostoma fasciculatum* (P) *Arbutus menziesii* (P) *Quercus kelloggii* (P) *Pinus sabiniana* Dougl. (P) *Rhus diversiloba*
	Mount Diablo, below Rocky Point, Contra Costa County	(P) *Ceanothus* sp.
	Jackson County, Oregon[2]	(P) *Arbutus menziesii*
P. densiflora subsp. *aurantiaca* (Benth.) E. F. Sprague	Lake Almanor, Plumas County	(C) *Pinus ponderosa* Dougl.
	Butte Meadows, Butte County	(P) *Pinus jeffreyi* Grev. & Balf. (P) *Abies concolor* Lindl. & Gord.
	Near Viola, Shasta County	(?) *Pinus ponderosa*
	Near Mineral, Tehama County	(?) *Pinus ponderosa*

TABLE 1, continued.

PEDICULARIS SPECIES	LOCALITY	HOST
P. attollens Gray	Tioga Pass, Mono County	(P) *Phleum alpinum* L.
	Slate Creek, Middle Ridge, Mono County	(C) *Carex heteroneura* W. Boott.
	Slate Creek, Timberline Station, Mono County	(C) *Carex heteroneura*
	Echo Pass (Phillips and one mile north), El Dorado County	(C) *Trifolium monanthum* Gray (P) *Phleum alpinum*
	Fallen Leaf Meadows, El Dorado County	(P) *Carex* sp.
P. groenlandica Retz.	Tioga Pass and Tioga Lake, Mono County	(C) *Carex helleri* Mkze. (C) *Deschampsia caespitosa* (P) *Carex fissuricola* Mkze.
	Slate Ridge, Middle Ridge, Mono County	(P) *Deschampsia caespitosa*
	Slate Creek, Timberline Station, Mono County	(C) *Poa* sp.
	Sonora Pass, Tuolumne County	(P) *Poa* sp.
	Norden, Placer County	(P) *Carex* sp.
P. crenulata Benth.	Convict Creek, Mono County	(C) *Deschampsia* sp. (C) *Trifolium monanthum* (P) *Poa* sp.
P. dudleyi Elmer	Portola State Park, Santa Cruz County	(P) *Vaccinium ovatum* Pursh (P) *Lithocarpus densiflora* (H. & A.) Rehd. (P) *Ceanothus thyrsiflorus* Esch.
P. racemosa Dougl.	Rainbow Tavern, Highway 40, Placer County	(P) *Abies concolor* (?) *Pinus monticola* Don.
P. semibarbata Gray	Above Lake Arrowhead, San Bernardino Mountains San Bernardino County	(C) *Pinus ponderosa*
	Mount San Gorgonio, at foot of trail to peak, San Bernardino County	(C) *Pinus ponderosa*
	Wrightwood, San Gabriel Mountains, San Bernardino County	(C) *Pinus ponderosa* (?) *Poa scabrella* (Thurb.) Benth.
	Mount Pinos, Kern County	(C) *Pinus ponderosa*
	Echo Lake, Eldorado County	(C) *Arctostaphylos patula* Greene
	Norden, Placer County	(?) *Abies concolor*

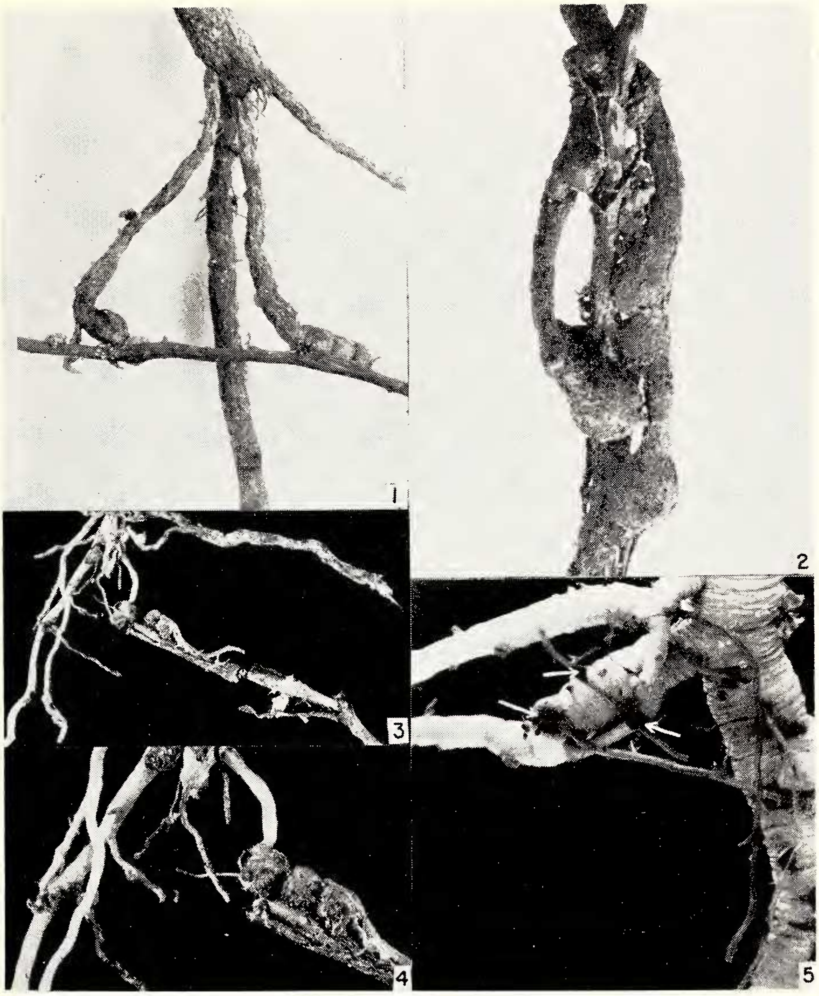
[1] All localities are from California except one, as stated, from Oregon.
[2] *Hitchcock 64988,* June, 1931 (RSA).

Santa Lucia Mountains, where two distinct populations associated with different hosts were observed within potential breeding range, the plants in each area appeared distinctive, although the difference could not be defined. In addition, *Pedicularis densiflora* subsp. *aurantiaca* seemed to be very nearly host specific; at least, haustoria were never found on roots of species other than *Pinus ponderosa*. *Pedicularis semibarbata,* likewise, was almost exclusively on *Pinus ponderosa;* at Echo Lake, El Dorado County, in an old burn, the nearest yellow pine was 80 feet away, but the *Pedicularis* was attached to its far-reaching roots.

Pedicularis densiflora and *P. semibarbata* have undergone an extreme divergence from a habitat of moist meadows and cool mountains such as that most species occupy to an almost arid habitat. The water requirements of such species must be critical. Under such conditions, woody shrubs and trees would provide both the most adequate supply throughout the growing season and an adjacent perennial root which could be annually tapped.

In addition to these close vascular plant associations, there seems to be some evidence that under more favorable climatic conditions certain species may be largely saprophytic or mycorrhizal rather than parasitic. On plants of *P. densiflora* at Phoenix Lake, Marin County, where humus and climate provide more continuously available moisture than in many areas within their range, very few small haustoria and no actual connections with adjacent plants were observed on six uprooted individuals. In a low drainage area near Viola, Shasta County, no haustoria were observed on *P. densiflora* subsp. *aurantiaca*. In both places, abundant mycelia in the rhizosphere suggested that mycorrhizae many function. Mycorrhizae may be important where species are largely saprophytic, also. The only material examined microscopically was taken from southern populations and showed no evidence of fungal elements.

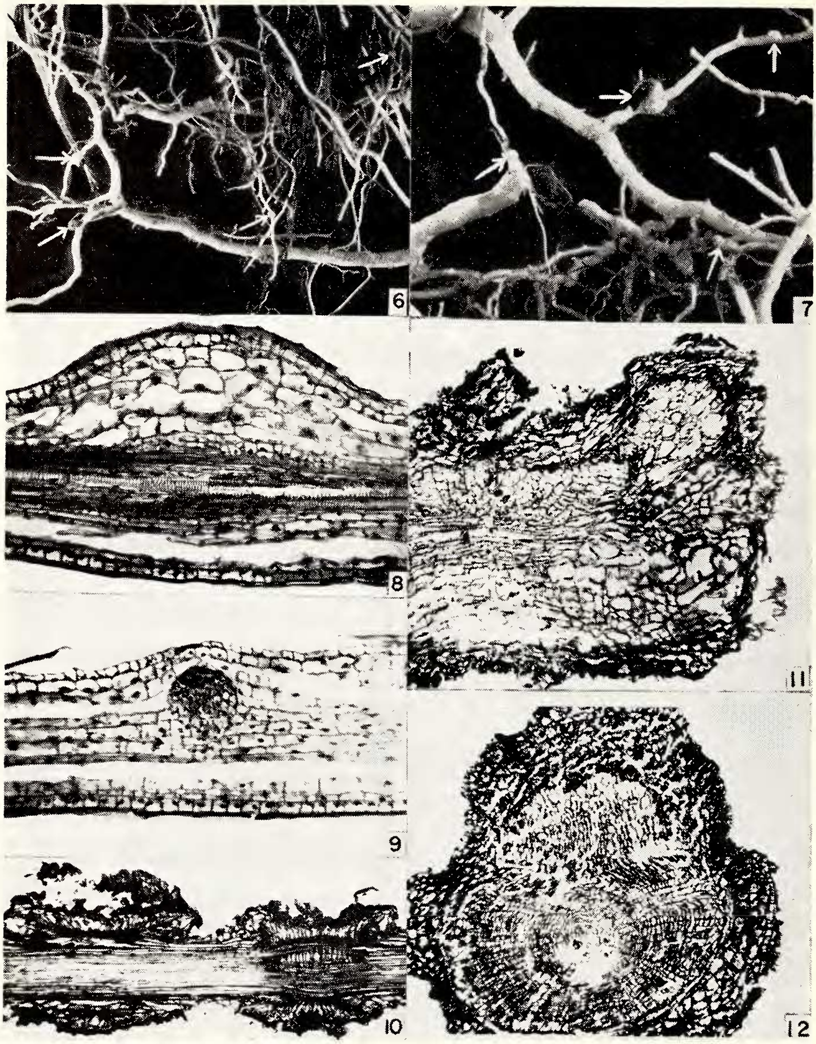
It was generally agreed among earlier investigators that members of the tribe to which *Pedicularis* belongs (Euphrasieae of Pennell, 1935; Rhinantheae of Wettstein, 1891) "take much from the earth" (Pitra, 1861, page 66, the quotation a translation from the German) and little from their hosts. Kerner (1895) observed the close contact of the epidermal cells with the humus. Hayek and Hegi (1918) reported that some species take organic materials to the detriment of the host. The importance of the host to the parasite is evidently due to a "disproportion between the parasite's water requirement and powers of the root to satisfy them" (Skene, 1924). Kostytschew (1922) showed that the cut shoots of *Euphrasia* absorbed water two times as fast, and those of *Melampyrum* ten times as fast, as the uncut shoots absorbed through their own roots. A similar distinction was found in the water absorption capacities of cut versus uncut shoots in *Pedicularis densiflora, P. semibarbata,* and *P. groenlandica*. According to Tubeuf (1923, page 564, referring to unpublished work of Senn and Hagler), *Euphrasia stricta*



FIGS. 1–5. 1, 2, haustoria of *Pedicularis densiflora* on *Adenostoma fasciculatum*, Del Mar, San Diego County; 3–5, haustoria of *Pedicularis semibarbata* on *Pinus ponderosa*: 3, Wrightwood, San Bernardino County; 4, 5, Mount Pinos, Kern County (note wrinkling of the large contractile root). (Fig. 1, × ⅝; 2, × ⅝; 3, × ½; 4, × 2; 5, × ½.)

Host. and *Pedicularis sylvatica* exhibit osmotic pressures significantly higher than those of their hosts. Although the loss of water to the parasite must put a considerable strain upon the absorbing system of the host, there are few references in the literature to any deleterious effects upon the host.

The nature of the haustorium was discussed and illustrated by Wettstein (1891), who considered it a reduced lateral root produced in the



Figs. 6–12. 6, 7, haustoria of *Pedicularis attollens* on *Poa* sp.; 8, median section through haustorium of *Pedicularis semibarbata* on *Pinus ponderosa*; 9, section through haustorial primordium of *Pedicularis attollens*; 10, longitudinal section of old haustorial connections of *Pedicularis attollens* on *Poa* sp.; 11, section of haustorium of *Pedicularis semibarbata* on *Pinus ponderosa*; 12, section of haustorium of *Pedicularis densiflora* on *Adenostoma fasciculatum*. (Fig. 6, × ½; 7, × 1½; 8, × 17; 9, × 25; 10, × 22; 11, × 15; 12, × 15.)

spring. Assimilation from the host continues through the summer, then the haustorial connection weakens. With resorption of the organic union with the host (fig. 10), the haustorium serves as a storage organ. According to Maybrook (1917), Leclerc du Sablon studied the haustoria in

1886 and concluded that they are exogenous in origin in both *Melampyrum* and *Pedicularis,* arising from peripheral parenchyma which is stimulated by contact with the host to multiply and by ordinary elongation penetrate the host, destroying the forepart and perforating the tissues by chemical absorption. Maybrook's work on *P. vulgaris* Tournef. led him to agree with these findings. The position of haustoria on rootlets of *P. groenlandica* and *P. attollens* (figs. 6, 7) would indicate that contact with the host stimulates production of haustoria. The present observations, however, agree with those of Wettstein (*op. cit.*), namely, that the haustoria are modified branch roots, endogenous in origin, and usually annual, as indeed they would have to be considering the contractile nature of the principal fleshy root system. However, observations on the very large haustoria of *P. densiflora* indicated they were the result of two or more years' growth.

Haustoria on all the species have a similar appearance; they are pale, fleshy lumps, usually occurring on the smaller branch roots. They vary in size with the species, with lesser variation between individuals of a given species. Large connections over 1 cm. in diameter of *P. densiflora* on *Adenostoma* (figs. 1, 2) are not frequent; they were found close to the "trunks" of the host and in the drier localities (Topanga Canyon and Del Mar mesa, table 1). The largest haustoria of *Pedicularis densiflora* subsp. *aurantiaca* on *Pinus* were 7 mm. in diameter. The haustoria of *Pedicularis semibarbata* (figs. 3–5, 11) were mostly small in comparison, but three of 4, 5, and 6 mm. were measured. Most haustoria observed on other species were very small, 1 to 3 mm. or less (figs. 6, 7), but even these small ones enclosed a large portion of the rootlets to which they were attached.

In transection the mature haustorium exhibits an outer zone of thick-walled tissue, lacunar collenchyma, then a wide cylinder of thick-walled parenchyma filled with starch and other material. The vascular cylinder consists of a comparatively wide outer phloem band and an inner core of protoxylem and metaxylem tracheids and vessels, together with considerable xylem parenchyma (figs. 8–12). A mass of short vessel elements arranged randomly intermingle with those of the host (figs. 11, 12), so that a most intimate and effective contact is made.

Sperlich (1902), in his examination of *Pedicularis* and related genera, frequently found tracheids wanting when the haustoria were saprophytic. He also identified storage products in addition to starch, such as albuminoid crystals, amylodextrin, phosphoric acid and nitrates, varying with the species and seasons. Examination of the present species under consideration showed starch and also large quantities of other products which had the appearance of albuminous material.

How early the haustorial attachment must be made probably depends on the vigor of the seedling as well as on the amount of soil moisture available. We do not know whether annual species are more or less dependent upon host plants than perennials are. Neither Prain (1891), who listed fourteen annual species in India, nor others have commented on this. The fibrous roots of *P. groenlandica* and *P. attollens* appear to have a greater number of haustoria than other California species observed; this may reflect a specific need for more food and water (although the former often grows in running water) from the host plant, or it may be that the smaller haustoria are less effective than the larger ones (e.g., those of *P. densiflora*). Also, this greater number may be an artifact of preparation; one can wash out the mass of *P. groenlandica* rootlets in a piece of sod more easily than one can dig extensive areas in the sun-baked hardpan of a chaparral-covered slope to obtain the entire root system of *P. densiflora*.

Seeds of *P. densiflora, P. semibarbata, P. groenlandica,* and *P. attollens* were germinated in loam. The seedlings were transplanted to humus, or in the case of *P. densiflora* and *P. groenlandica,* to pots containing appropriate host plants. None of these became established nor did the roots develop macroscopic haustoria. Lack of success in establishing seedlings and in transplanting these species was probably due in part to their parasitic nature and to the lack of adequate haustorial connections or of an appropriate host.

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